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Peleophycus multiprocarpium gen. et sp. nov. (Gloiosiphoniaceae, Rhodophyta)[1]

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ABSTRACT: *Peleophycus multiprocarpium* is described as a genus and species new to the red algal family Gloiosiphoniaceae (Cryptonemiales), in which a given supporting cell may bear one or more carpogonial branches and one to several auxiliary cell branches. Though several gonimoblasts could thus be formed on the same supporting cell, this condition has not been observed. Nonetheless it suggests a possible phylogenetic pathway from less complicated to more complex relationships of reproductive branches. In its structure of reproductive organs, *Peleophycus* seems most closely related to *Gloeophycus*, described from Korea and northwestern Japan. *Peleophycus* is one of several new genera and species that occurred in an unexpected subtidal (ca. 10–12 m depth) spring marine flora in the subtropics off Hawaii.

THOUGH THE DETAILS OF postfertilization events in many Florideophyceae are essentially in the same state of knowledge as described by Kylin (1956), information on others, particularly members of the Ceramiales (Wollaston 1968, Gordon 1972) and the austral Gigartinales (Kraft 1975, 1977*a*, 1977*b*, 1978), has added dimension to our knowledge as well as substantiated the major lines of the classification of Kylin (1956). The elegant studies of Kraft have shown postfertilization events that have resulted in very complex and massive carposporophytes that surely surpass in interest and phylogenetic implications the vegetative nature of the auxiliary cell that has been described as central to their development.

While with very few exceptions, the vegetative nature of the auxiliary cell is clear in the Gigartinales, in the Cryptonemiales the derivation and evolution of this cell are frequently controversial (Lebednik 1977) or not wholly understood. In its simplest form, so well exhibited, for example, by either *Dudresnaya* (Littler 1974) or *Acrosymphyton* (Hawkes 1982), the auxiliary cell is carried in an intercalary or terminal position, respectively, in a uniseriate, unbranched (rarely branched) filament. This filament is in addition to an already established pattern of vegetative branching. This is the meaning of "auxiliary cell in an accessory or specialized filament" (translated from Kylin 1930, 1956). In the Kallymeniaceae (Norris 1957), a nearly complete evolutionary series is exhibited by various species: from auxiliary cells and carpogonial branches on different and separated supporting cells requiring connecting filaments to transfer the diploid nucleus, to a loss of subsidiary elements and a final uniting of one functional carpogonial branch per auxiliary cell, without connecting filaments, which is seen in six species of *Callophyllis* from the Pacific coast (Abbott and Norris 1965). Without the intervening evolutionary series, it would be difficult if not impossible to derive the auxiliary cell, which is the supporting cell, as a cell of accessory origin in these "monocarpogonial" species. The Corallinaceae (Lebednik 1977) perhaps show the same type of evolutionary loss, fusion, and regrouping that is more difficult to interpret than is the situation in the Kallymeniaceae.

The topographic relationship of the carpogonial branch and the auxiliary cell branch is one of the important features of the reproductive structures in the Cryptonemiales. While the Kallymeniaceae and Corallinaceae may be the most advanced taxa in the two

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evolutionary series within the Cryptonemiales of Kylin (1930:98), each of these series has primitive members that vegetatively resemble each other. The series which is topped by the Kallymeniaceae has the Gloiosiphoniaceae as the primitive member because of its uniaxial structure and the union (with one exception) of carpogonial and auxiliary cell branches on the same supporting cell. This is the procarpial series which implies evolutionary ties to advanced red algae that always have the auxiliary cell closely tied to the carpogonial branch. The primitive family in the other, nonprocarpial, series is the Dumontiaceae in which thalli are mostly uniaxial and the carpogonial branch may be 100–300 μm distant from the auxiliary cell branch, thus requiring lengthy and sometimes elaborate connecting filaments for conveying the diploid nucleus (*Acrosymphyton*, Abbott 1962*b*). Necessarily, there are two separate supporting cells. The shortening of connecting filaments and the congestion of female reproductive structures is observed in the crustose Peyssoneliaceae (Hollenberg and Abbott 1968), where, as is common also in *Farlowia* (Abbott 1962*a*) in the Dumontiaceae, the number of auxiliary cell branches is greater than the number of carpogonial branches in fertile areas.

The simplest procarpial condition may be seen in the Gloiosiphoniaceae (Kylin 1930) in which the carpogonial branch and auxiliary cell branch are borne in the same fertile branch (*Gloiosiphonia*) or on the same supporting cell, adjacent to each other. In the four genera in the family, only one, *Gloiosiphonia*, retains connecting filaments (Edelstein 1972), thus clearly relating this family to the Dumontiaceae. In the remaining three genera, the diploid nucleus is transferred without connecting filaments from the carpogonium to the adjacent auxiliary cell. In two of the genera, *Gloiosiphonia* Berkeley and *Thuretella* Schmitz, the auxiliary cell is intercalary in position, and in the two remaining taxa, *Schimmelmannia* Kuetzing and *Gloeophycus* Lee and Yoo, it is terminal. In both of the latter genera, connecting cells which are cut off from the fertilized carpogonium form a bridge to the auxiliary cell. Except for some connecting cell differences in *Schimmelmannia plumosa* (Umezaki 1967), there appears to be very little variation within each taxon with respect to these fertilization events.

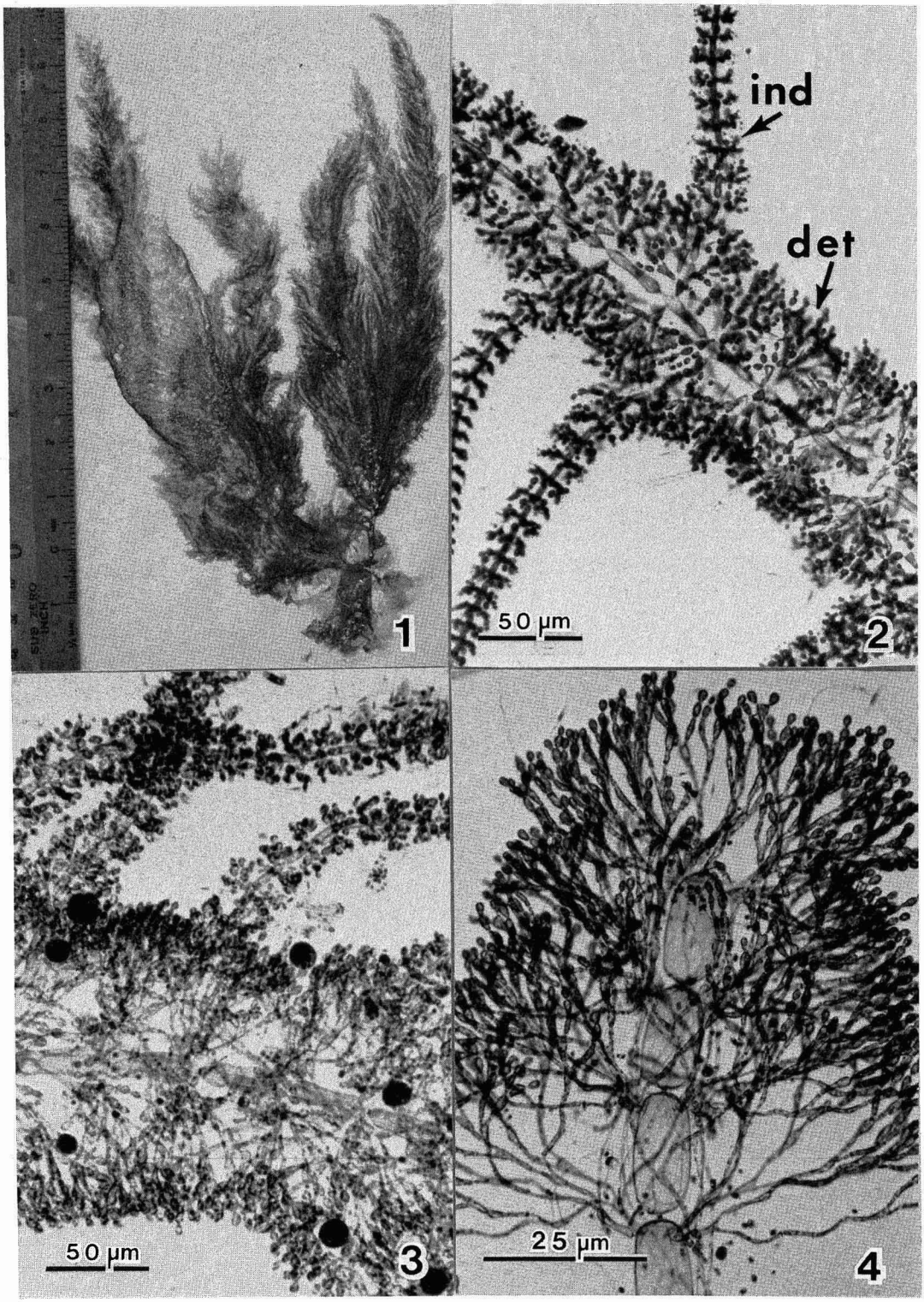
A new genus in the Gloiosiphoniaceae is described here which shows one to several carpogonial branches with one to many auxiliary cell branches on the same supporting cell, with the immediate postfertilization event in which a sister cell of the carpogonium fuses with an auxiliary cell in an adjacent auxiliary cell branch.

Peleophycus genus nova

Thalli (Figure 1) uniaxiales, fortiter mucosi, ramosis indeterminatis ramis laxe ferentibus ramulos densos (Figure 3). Rami ultimi verticillis 4 lateralibus determinatis (Figure 2) affixis prope apicem cellularum axialium (Figure 4). Cellulae basales laterales et pro parte maxima cellulae axiales rhizoidea descendentia quae adiciunt ad crassitiem thalli ferunt. Monoici. Spermatangia (Figures 8, 9) sine pedicellis, 1–3 formata e omni spermatangiali materna cellula. Rami carpogoniales (Figure 5) et rami auxilliares (Figure 6) cellulares curvati leviter ad valde, multi formati in omni cellula sustinenti. Post fecundationem, carpogonium cellulam coniungentem abscidit quae cum contigua terminali axillari cellula coniungit. Carposporangia producta in gonimolobis (Figure 7), fere omnia sed cellulae basales crescentes in sporas.

Thalli uniaxial, strongly mucosoid, densely branched, with irregular numbers and disposition of indeterminate branches; each order of branches pinnate. Ultimate branches with whorls of 4 determinate laterals attached near the apex (Figure 4) of axial cells, additional laterals may be added with age; a fifth or sixth element in the form of an indeterminate branch may occur irregularly, forming short flagelliform branches (Figures 2, 3). In older axes, all basal cells of laterals and most axial cells bear descending rhizoids which add to the thickness of the thallus.

Monoecious. Spermatangia without stalks, 1–3 formed (Figure 9) from each spermatangial mother cell. Carpogonial branches and auxiliary cell branches slightly to strongly curved, many formed on each supporting cell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which is the basal cell of a lateral (Figure 10), or a special cell attached to the basal cell of the lateral, or to the basal cell of the next order of branchlets. One, two, three, or all four basal cells of laterals may bear carpogonial and auxiliary cells. Carpogonial branches (Figure 5) lightly staining, of 4–5 cells; auxiliary cell branches conspicuous (Figure 6), of 2–4 cells. After fertilization, the carpogonium cuts off a sister cell which becomes a connecting cell that fuses with an adjacent auxiliary cell that is a terminal cell of the auxiliary cell branch. Carposporangia (Figures 7, 10) produced in gonimolobes, nearly all but the basal cells becoming spores. No involucre or sterile filaments occur around the carposporophyte.

The genus is named for the Hawaiian fire goddess, Pele, who, according to legend, produces all the basalt rock around the Hawaiian Islands. Basalt is the only substratum upon which *Peleophycus* is known to occur.

TYPE SPECIES: *Peleophycus multiprocarpium*.

Peleophycus multiprocarpium sp. nov.

Thalli cum uno vel pluribus axibus percurrentibus, ramificantes in modo irregulariter radiali. Ultimi rami flagelliformes frequentes prope apices, alterni vel laxe spirales. Monoici. Spermatangia restricta in terminales cellulas ramorum brevium indeterminatorum, 1–3 ad quoque cellulam maternam, sine pedicellis. Rami auxiliares cellulares 1 ad plures pro quoque ramo carpogoniale. Post fecundationem, carpogonium dividens semel, proximalis cellula agens velut cellula coniungens cum proximali terminali cellula axillari. Gonimoblastus constans ex pluribus gonimolobis, simul omnibus maturescentibus.

HOLOTYPE: Abbott 16289, a single specimen and prepared microscope slide (BISH), collected by Jane Lewis and James Berdach off Shark Cove, Pupukea, NW Oahu Island, Hawaii, 18 May 1983. Isotypes under the same number (US, UC, MELU, SAP, PAR), and a syntype (Abbott 16306) from Shark Cove, Pupukea, Oahu Island, 21 May 1983, leg. Karla McDermid (BISH).

Thallus mucosoid, dark rose to brownish red; main axes 2–3 mm diameter when dried. Fronds 8–14 cm tall, with a single axis on which long, indeterminate branches are irregularly formed, or the axis early divided into 2–several leading axes. Main branching orders three, irregularly pinnate, the last order bearing determinate whorls of laterals, occasionally interrupted by irregular ultimate branchlets less than 1 mm long. These indeterminate branches arise in addition to the four laterals in a whorl and are formed alternately or may describe a loose spiral from every fourth segment. They are restricted to the upper third of the thallus. In older portions of the thallus, judged by the abundance of rhizoids, elongate laterals, and numerous endophytes; some laterals retain the capacity to form anew these flagelliform branchlets on which spermatangia and developing female reproductive structures are observed.

Internally, fronds uniaxial, each axial cell when young bearing 2–3 and finally 4 whorled laterals attached to the distal end of the axial cells. Laterals about 10 segments from the apical cell approximately 15 μm long; in the region of developing carposporophytes, ca. 100 μm long, 4–5 times irregularly di-trichotomously branched, the ultimate cells beadlike, about 5 μm, remaining close to that size through the aging plant. Colorless hairs

FIGURE 1. Gross habit of the holotype (BISH) of *Peleophycus multiprocarpium*, showing several leading percurrent axes pinnately branched.

FIGURE 2. Upper portion of axis 2 mm from apex showing irregularly positioned indeterminate (ind) branches among the whorled laterals or determinate (det) branches.

FIGURE 3. Portion of axis 1 cm from apex showing radial elongation of determinate branches and thickening around axial strand by the formation of rhizoids. Black dots are epiphytes.

FIGURE 4. Portion of indeterminate lateral 2 cm from apex of old thallus showing elongate whorls of laterals (determinate branches) and very inflated axial cells.

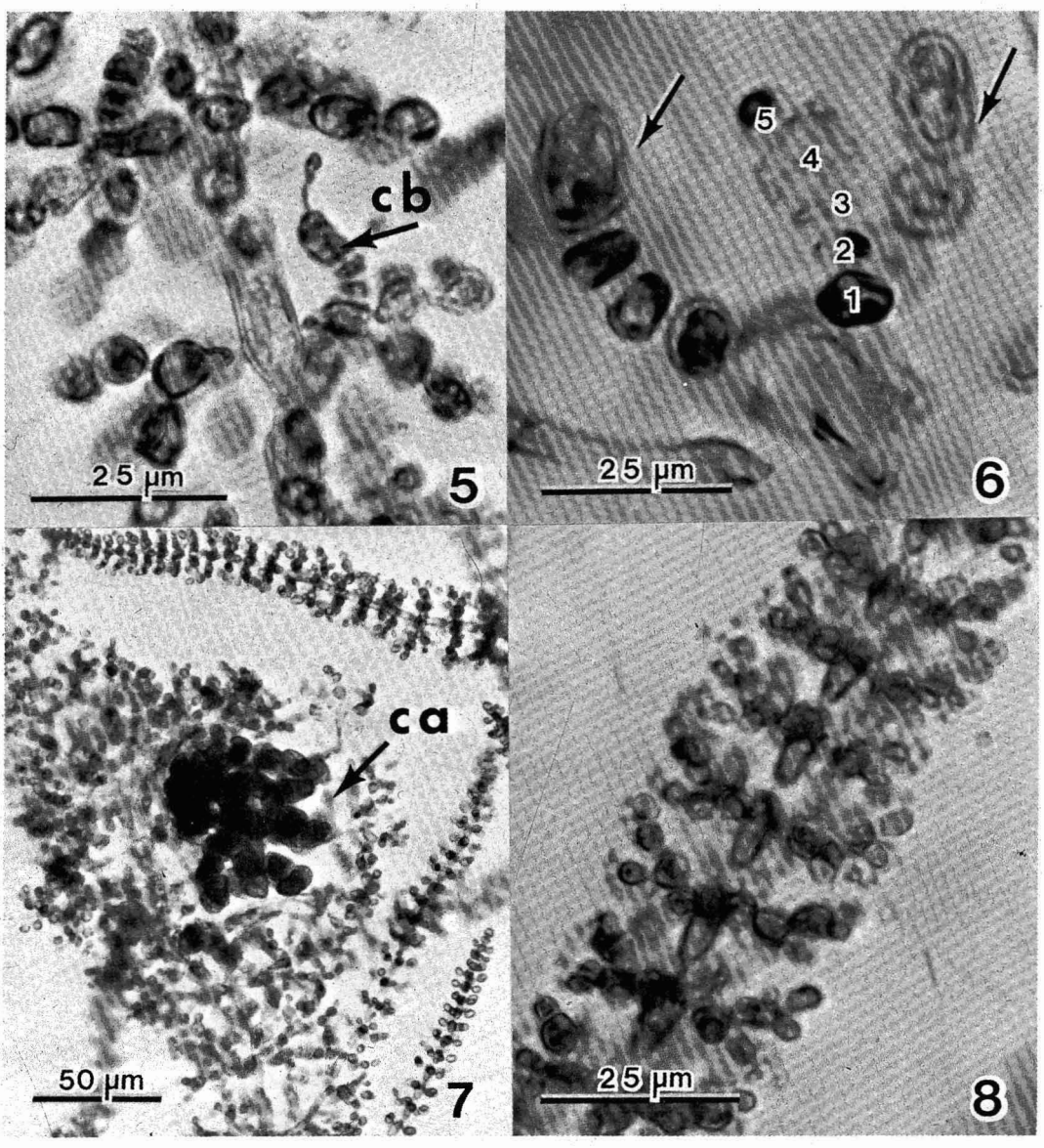

FIGURE 5. Young axis showing earliest carpogonial branch (cb); in this region, auxiliary cell branches have occurred first.

FIGURE 6. Auxiliary cell branches (arrows) and one carpogonial branch with the trichogyne out of view (cells 1–5 of the carpogonial branch correspond to the darkly stained basal cell, followed by cells 2 and 3 which are small and pale, cell 4 which is the enlarged hypogynous cell, and cell 5 which is the carpogonium).

FIGURE 7. Cystocarp within thallus, producing a slight bulge. Carpospores (ca) are released freely, without a carpostome.

FIGURE 8. Young indeterminate branch with spermatangia.

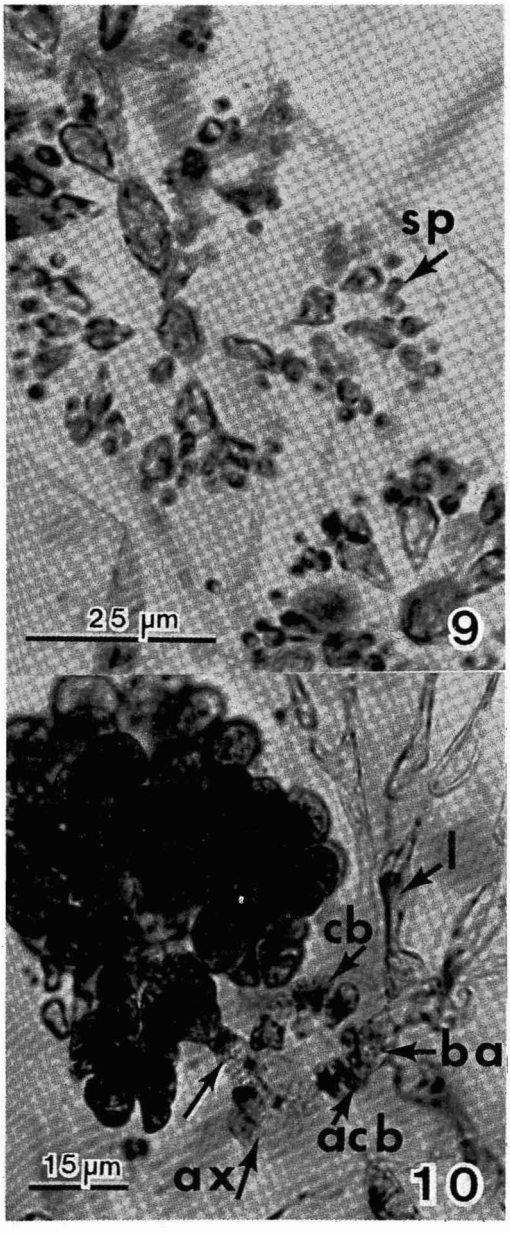

FIGURE 9. Lateral (upper) view of spermatangia (sp) and polar view of spermatangial branch from a young indeterminate branch.

FIGURE 10. Cystocarp showing basal cell (ba) of lateral (1) bearing auxiliary cell branch (acb) and carpogonial branch (cb) forming a pedicel for the gonimoblast (arrow). The axial cell (ax) is also shown.

occur near the apex and are rare. About 1 mm from the apex, cells of the central axis bear laterals of 5–6 whorls, the lower cells of most of these producing downwardly directed rhizoids. Rhizoids are of two sorts: those from the axial cells about 10 µm wide and 45 µm long, continuing for one to several mm; those from the basal cells of laterals, 30 µm wide and 90–135 µm long, the filaments sometimes branching but rarely longer than 1 mm. Rhizoids from laterals are more numerous than those from the axial cells. Laterals in these rhizoidal areas are 390–450 µm long, showing about 7 dichotomies, the cells frequently no more than 5 µm in diameter and 3–4 times longer than the diameter. In these regions the cells of the central axis have enlarged from 16 µm to 53–60 µm and are more cylindrical where similar cells were previously oval.

REPRODUCTION: Monoecious. Spermatangia about 2 µm diameter, 1–3 produced by each spermatangial mother cell, without stalks. Spermatangia restricted to terminal cells of laterals within 0.5 mm of apex in the main axes, or to the flagelliform indeterminate branchlets that are irregularly formed. Carpogonial and auxiliary cell branches slightly to strongly curved, attached to basal cells of laterals, or to supporting cells borne on these basal cells, and occasionally to basal cells of the next higher order, but the latter never observed with postfertilization stages. Each fertile node shows 1 or all 4 basal cells with at least 2 (up to 8) auxiliary cell branches, and one or two carpogonial branches. In any given fertile cluster, auxiliary cell branches vary in the number (2–4) of cells they contain; only those with at least 4 cells have been observed at the base of gonimoblasts. There are 1–6 auxiliary cell branches for every carpogonial branch that is formed within a fertile node. Carpogonial branches lightly staining, of 4–5 cells, the second from the base usually very small, about 1/2 the diameter of the basal cell; the hypogynous cell sometimes twice the diameter of the carpogonium, and frequently more deeply staining than the remainder of the cells in the branch; the terminal carpogonium slightly bent, the contents colorless and granular; with a relatively short trichogyne.

Auxiliary cell branches 3–5 cells long, all cells but the terminal one deeply staining, the terminal cell (the auxiliary cell) obovate and 13–22 μm diameter.

After fertilization, the carpogonium divides once, the lower of the two cells so formed (a connecting cell or sister cell of the carpogonium) fuses with the auxiliary cell which cuts off from its distal surface the gonimoblast initial and after repeated divisions, forms several gonimolobes containing carposporangia, each about 20 μm in diameter. Though dividing in groups, carposporangia mature at about the same time, and only rarely do they show maturation sequentially within the cystocarp. No sterile filaments occur within the region of the cystocarp.

DISCUSSION

A variety of ways for transferring the diploid nucleus in a carpogonium or a sister cell to an auxiliary cell is displayed by species included in the lower families of the Cryptonemiales (the Dumontiaceae and Gloiosiphoniaceae). As might be expected of primitive taxa, neither the position of the fertile branches nor the order of cells in them is as uniform as they are in the families of Ceramiales (Kylin 1956). In the Gloiosiphoniaceae, *Gloiosiphonia* shows the most variability in the female reproductive structures, the supporting cell for the carpogonial branch and auxiliary cell branch being undefined, the number of cells in the auxiliary cell branch unpredictable, the actual cell that is to function as the auxiliary cell unclear until after diploidization, and the number of sterile laterals on this branch varying as well (Edelstein 1972, Abbott 1950). Though attached to a common supporting cell with the auxiliary cell branch, the carpogonial branch in *Gloiosiphonia* may contain three or four cells, the number varying on the same branch system whether borne singly or in pairs (Kylin 1930, Edelstein 1972). *Gloiosiphonia* is particularly interesting because after fertilization, the carpogonium puts out connecting filaments that are to convey the diploid nucleus or a daughter nucleus to an auxiliary cell, not necessarily in the same branch system. This is the crux of the Kylin (1956) interpretation of a procarp: the close proximity of the carpogonium to the auxiliary cell requiring the deposition of the diploid nucleus in the adjacent auxiliary cell. Since *Gloiosiphonia* has connecting filaments (as in the Dumontiaceae), the female reproductive system is not procarpic. A similar relationship is shown by some of the Kallymeniaceae which Norris (1957) divided into nonprocarpic and procarpic types. *Gloiosiphonia*, then, has one of the elements of a procarp, the uniting of the two fertile elements on the same fertile branch but not adjacent to each other. However, the remaining genera in the Gloiosiphoniaceae, *Schimmelmannia*, *Gloeophycus*, and *Peleophycus*, do not produce connecting filaments and therefore the close proximity of carpogonial and auxiliary cell branches assumes a new importance. In these three genera, connecting cells are formed that connect the carpogonium with the adjacent terminal auxiliary cell. Following the interpretations of Kylin (1930, 1956) these taxa are clearly procarpial. *Thuretella* differs from these three genera only in having an intercalary auxiliary cell. Though two carpogonial branches per auxiliary cell have been observed in *Schimmelmannia* (Abbott 1961) and *Gloeophycus* (Kaneko, Matsuyama, and Yamada 1980), nuclear transfers apparently involve only one carpogonial branch for each auxiliary cell. Similarly, multiple auxiliary cells in the same fertile system, some occurring with several carpogonial branches per auxiliary cell, are demonstrated by the procarpial species in the Endocladiaceae by *Gloiopeltis furcata* and *Endocladia muricata* (Kylin 1930, fig. 8, and Kylin 1928, fig. 23, respectively). The compound auxiliary cell branches of *Leptocladia binghamiae* (Abbott 1968, fig. 32), borne on separate branches from the carpogonial branch (and thought to be functionless, but never further tested), may be a simpler arrangement of potential auxiliary cells.

Peleophycus, in terms of its female reproductive structures, is more closely related to *Schimmelmannia* and *Gloeophycus* because of the formation of a connecting cell following fertilization. However, the multiplicity of auxiliary cell branches and thus the potential of a

large number of developing procarps is very different from these two genera where single auxiliary cell branches occur with single (rarely two) carpogonial branches. With many auxiliary cell branches, it is potentially possible to have many procarpic relationships, and thus many gonimoblasts. The fact that the number of carpogonial branches has been reduced may indicate that there is a taxon that may show a one to one relationship of these two branch systems on the nonspecialized lateral. Or, that there is a taxon that may show the same relationship of these branches as obtains in *Peleophycus*, but postfertilization involves connecting filaments, perhaps to auxiliary cells in sequence, therefore like the Dumontiaceae. Vegetatively, the plants do not resemble other Gloiosiphoniaceae in branching pattern or aspect, but strongly resemble, in either the dried or preserved state, species of *Acrosymphyton* (Dumontiaceae). In Hawaii, however, *Acrosymphyton* species are twice to three times the size of *Peleophycus*. The single most conspicuous difference is in the widely separated carpogonial and auxiliary cell branches in *Acrosymphyton* and the elaborate network of connecting filaments, making multiple diploidization possible.

The attachment of the reproductive branches is an important feature of the more advanced red algae, such as members of the Ceramiales, in which the order of appearance of the pericentral cells (equivalent to the basal cells of laterals) is frequently used to distinguish families and genera. The reproductive structures are cut off in turn in predictable sequences (cf. Gordon 1972). In the Dumontiaceae, it is clear that the relationship of fertile and sterile branches is not yet fixed. For example, in *Acrosymphyton* (Kylin 1930, Hawkes 1982) the carpogonial and auxiliary cell branches occur on axial cells in no special locations or sequences. From the available evidence in the Gloiosiphoniaceae (Kylin 1930), it appears that the union of the fertile branches occurred before a fixed pattern of their relationship to sterile vegetative elements was established. This is nowhere more clear than in *Peleophycus* where the carpogonial and auxiliary cell branches are attached directly to the basal cell of a lateral of the first or second order and occasionally to a daughter cell of the basal cell. In other words, there are no special systems of fertile branches in *Peleophycus*, only the fertile branches themselves. Were it not for the occasional daughter cell (a supporting cell) carrying the two fertile branches, *Peleophycus* could not be allied to the Gloiosiphoniaceae as presently delimited since in no other taxon is the supporting cell the basal cell of a lateral. This condition is more true for the Dumontiaceae (Kylin 1928, in *Cryptosiphonia*) where the auxiliary cell branches and carpogonial branches arise directly from secondary axial cells (also see Smith 1938). A review of microscope slide material in the author's slide collection of species of *Schimmelmannia*, *Thuretella*, *Gloiosiphonia*, and *Gloeophycus* indicates that all taxa show the supporting cell to be at least one or two cells removed from the basal cell of the lateral.

Peleophycus is one of several newly recognized taxa that occurred with two rarely collected subtidal Hawaiian algae at depths of 10–12 m in the spring of 1983. Of the two known taxa, *Acrosymphyton taylori* Abbott and *Dudresnaya hawaiiana* Lee, *A. taylori* occurred attached to rock in large quantities, about 30 herbarium sheets being prepared from one dive. Though the type specimen was collected attached, all subsequent collections until now have been made from drift material. These two genera are also known to be spring annuals in Bermuda (Taylor 1960). In the case of *Peleophycus*, no other member of the Gloiosiphoniaceae is known from the subtropics or tropics. Whether or not it is a seasonal plant is not known; repeated visits to the same locality through the summer and fall of 1983 showed no further specimens.

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